

Quantifying the Robustness of a Broth-Based Model for Predicting *Listeria monocytogenes* Growth in Meat and Poultry Products

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ABSTRACT

Given the importance of *Listeria monocytogenes* as a risk factor in meat and poultry products, there is a need to evaluate the relative robustness of predictive growth models applied to meat products. The U.S. Department of Agriculture–Agricultural Research Service Pathogen Modeling Program is a tool widely used by the food industry to estimate pathogen growth, survival, and inactivation in food. However, the robustness of the Pathogen Modeling Program broth-based *L. monocytogenes* growth model in meat and poultry application has not, to our knowledge, been specifically evaluated. In the present study, this model was evaluated against independent data in terms of predicted microbial counts and covered a range of conditions inside and outside the original model domain. The robustness index was calculated as the ratio of the standard error of prediction (root mean square error of the model against an independent data set not used to create the model) to the standard error of calibration (root mean square error of the model against the data set used to create the model). Inside the calibration domain of the Pathogen Modeling Program, the best robustness index for application to meat products was 0.37; the worst was 3.96. Outside the domain, the best robustness index was 0.40, and the worst was 1.22. Product type influenced the robustness index values ($P < 0.01$). In general, the results indicated that broth-based predictive models should be validated against independent data in the domain of interest; otherwise, significant predictive errors can occur.

Quantitative risk assessments for the fate of pathogens in food products depend heavily on the validity of predictive models for pathogen growth, survival, and inactivation. An accurate prediction may require a consideration of whether a model is easy to use (the simplest one for a given purpose and data quality), whether it is robust and accurate (it must reflect reality), and whether it is validated against independent data sets (19). The validation or performance evaluation of a model can also be referred to as the robustness of the model (6). The robustness indicates how well a model predicts future independent results across a wide domain of conditions. However, experimental data and associated models are rarely available to account for all of the relevant variables and range of conditions for a specific pathogen, product, and process being analyzed. Therefore, a risk assessment might extrapolate the predictive models, either in terms of the process parameters (e.g., temperature) or product parameters (e.g., fat content). Even though this practice is fundamentally undesirable, it might be the only means to complete a risk assessment for a given product or system; therefore, it is desirable and necessary to fully understand the implications of this practice.

In particular, given the importance of *Listeria monocytogenes* as a risk factor in ready-to-eat meat and poultry products, there is a need to evaluate the relative robustness

of predictive microbial growth models for this specific pathogen. Previous research has shown that product and process variables (e.g., pH, water activity [a_w]) significantly affect *L. monocytogenes* response (7). However, knowing that an effect exists is not sufficient to account for that effect quantitatively in predictive models. Some studies have reported only descriptive models (meaning that experimental data are generated, and a model is fit to those data), which describe the combined effect of temperature, pH, a_w , and CO₂ concentrations (11, 27). Other investigators have compared their mathematical models (of the effect of CO₂, pH, temperature, NaCl, organic acids, and modified atmospheres) against independent data sets (4, 12, 13). Unfortunately, they made only qualitative comparisons between observed and predicted values and did not present a quantitative validation for their models.

On the other hand, Ross (20) presented the bias and accuracy factors as indices to evaluate the performance of predictive models in food microbiology in terms of growth parameters (i.e., growth rates and lag-phase duration). The bias factor is an overall average of the ratio of discrete model predictions to observations and assesses whether or not the model is “fail-safe,” “fail-dangerous,” or perfect. The accuracy factor is similar to the bias factor, except that it is the absolute value of the ratio of predictions to observation, thus providing an accumulated measure of overall model accuracy. However, these factors have only been

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TABLE 1. *References and keys in ComBase for meat and poultry products*

Data set no.	Key (ComBase)	Product type	Reference
1–6	J206_Lm to J211_Lm	Ground beef	18
7–12	J232_Lm to J237_Lm	Cooked chicken	1
13	M007	Pate	3
14–18	M200_LM to M204_LM	Cooked pork	10
19	M263_LM	Precooked beef	8
20–24	M263_Lma to M263_Lme	Precooked beef	8
25–26	M656_LM to M657_Lm	Cooked beef w/gravy	14
27–28	M660_Lm to M661_Lm	Cooked beef w/gravy	14
29	M921_LM	Home-style salad (chicken with no mayonnaise added)	9
30	M921_LMa	Home-style chicken salad	9
31	M921_LMb	Home-style salad (real mayonnaise + chicken)	9
32	M921_LMd	Home-style salad (reduced-calorie mayonnaise + chicken)	9
33	M921_LMg	Home-style salad (real mayonnaise + chicken)	9
34	M921_Lmi	Home-style salad (reduced calorie mayonnaise + chicken)	9
35	SL113	Turkey	16
36	SL118	Turkey	16
37	SL123	Turkey	16
38–41	SL59 to SL62	Pork	16
42–52	M122_133 to M122_144	Pate or ham	26
54–65	M122_37 to M122_48	Pate or ham	26

used to evaluate the performance of secondary models in predicting growth parameters; actual log counts (from primary plus secondary models) were not considered.

The true measure of product safety is actual microbial counts, not model parameters. Campos et al. (6) introduced a new methodology to evaluate the robustness of a microbial growth model in terms of microbial counts. The robustness index (RI) was defined as the ratio of the standard error of prediction to the standard error of calibration. The standard error of calibration and standard error of prediction are the root mean square errors calculated from the original and independent data sets, respectively. The root mean square error is one of the most useful and informative measures of the goodness-of-fit against the model prediction for linear and nonlinear regressions. Moreover, it is a way to estimate the discrepancy between the observed and predicted data, which reflects whether a model truly fits the data well (15). A robust model will have an RI value near to or less than 1, meaning that the overall performance of a microbial model tested against an independent data set is within the expected error (standard error of calibration) of the model. Campos et al. (6) also stated that the RI value alone does not tell whether the observed values are above or below the predicted values; therefore, the mean relative error (RE) is used with the RI to provide this information.

The U.S. Department of Agriculture–Agricultural Research Service (USDA-ARS) Pathogen Modeling Program (PMP) (25) and the UK Food MicroModel are tools used by the food industry to estimate pathogen growth, survival, and inactivation in food. Most of these models were developed from pure-culture, broth-based data. Because these models are based on pure-culture systems containing high levels of nutrients and no competitive microbial flora, they are generally assumed to provide conservative estimates of pathogen growth.

Several authors have considered the performance of the

PMP and other microbial growth models. For instance, te Giffel and Zwietering (24) evaluated the prediction of *L. monocytogenes* growth rates in foods, including meat, by general models (e.g., Gamma-concept, PMP, Food MicroModel) and by specific models (e.g., modified Arrhenius equation, third-order polynomial model, quadratic equation). They tested these models against independent data sets and validated the models by graphical comparison and mathematical and statistical comparison (mean square error, regression coefficient, bias, and accuracy factors). They recommended the use of a set of criteria to evaluate the performance of models, because the use of one criterion may fail to reveal some forms of systematic deviation between observed and predicted behavior. Again, the prior study evaluated the performance of only a secondary model; actual log count predictions were not evaluated.

Additionally, the evaluation of these models did not include data outside their original domain, which is critically important if they are to be applied to broader risk analyses for foodborne pathogens in ready-to-eat food products. Furthermore, the prior studies evaluated only secondary models for growth parameters (i.e., growth rate, generation time, lag-phase duration). They did not evaluate the robustness of the complete model (primary plus secondary), which predicts the actual growth values and gives the complete behavior (lag phase, exponential growth, and stationary phase) of the pathogen of interest.

Therefore, the objective of the present study was to evaluate the robustness, against independent data, of the PMP broth-based growth model for *L. monocytogenes* in meat and poultry products in terms of predicted microbial counts that covered a range of conditions inside and outside the original model domain.

MATERIALS AND METHODS

Data sources. ComBase (2, 26) was used as the main source of independent data sets. ComBase predistribution version 2002

TABLE 2. Coefficient values for secondary models^a

Variable	Aerobic		Anaerobic	
	Ln GT	Ln LPD	Ln GT	Ln LPD
Intercept	21.45832	26.86796	13.51036	19.82645
<i>T</i>	−0.26798	−0.21535	−0.10334	−0.20281
pH	−5.29657	−6.5596	−3.34632	−4.34946
NaCl	0.012824	0.051605	0.042326	0.031356
NO ₂	0.020202	0.019974	0.021956	0.024464
<i>T</i> × pH	0.00757	0.003684	−0.01424	−0.0032
<i>T</i> × NaCl	7.94E-06	0.000223	−3.5E-05	7.06E-05
<i>T</i> × NO ₂	−5.1E-07	1.93E-05	4.83E-06	1.62E-05
pH × NaCl	−0.00137	−0.00686	−0.0036	−0.00181
pH × NO ₂	−0.00278	−0.0028	−0.00282	−0.00321
NaCl × NO ₂	5.28E-06	−3.7E-06	4.14E-06	−2.7E-06
<i>T</i> ₂	0.00266	0.001918	0.002725	0.003123
pH ²	0.384181	0.487334	0.262941	0.310527
NaCl ²	0.000122	0.000102	−0.00027	−2.6E-05
NO ₂ ²	5.91E-07	7.36E-07	−8.6E-07	−4.8E-07

^a GT, generation time; LPD, lag-phase duration.

was searched for all records that included microbial counts with organism: "*L. monocytogenes/innocua*," and broth or food category: meat or meat products. In total, 65 data sets were found; 41 were within the domain of the PMP *L. monocytogenes* growth model, and 24 were outside the domain of the model (Table 1).

The original data sets used to develop the PMP broth-based *L. monocytogenes* growth model were also obtained from ComBase (26); source: "Buchanan_90," organism: "*L. monocytogenes/innocua*," environment: "culture medium," pH: "0.1 to 14," temperature: "−25 to 120°C," and *a*_w: "0.01 to 1." These data sets were assumed to be the original ones used in the PMP, because they were in the same range of experimental conditions (pH: 4.5 to 7.5, nitrite: 50 to 1,000 ppm, salt: 15 to 50 g/liter, and temperature: 5 to 37°C) and had a similar number of data sets (385 for anaerobic and 553 for aerobic). The no-growth data were eliminated (4, 5). The remaining data sets (*n*_{sets} = 291, *n*_{points} = 2,302 for anaerobic, and *n*_{sets} = 476, *n*_{points} = 3,680 for aerobic) were used to calculate the standard error of calibration of the PMP growth model.

Predictive models. The robustness of the *L. monocytogenes* in broth-culture (NaCl), aerobic and anaerobic, growth models in PMP version 7.0 (25) was determined by testing the model predictions against the independent data sets. Because the PMP, as it is distributed, cannot run outside the calibration domain, the secondary models used to calculate generation time and lag-phase duration within the PMP domain (Table 2) were implemented in a spreadsheet (source: A. Pickard, USDA-ARS Eastern Regional Center) to generate predictions for the data sets that were outside the original domain.

The primary model was the Gompertz equation:

$$L(t) = A + Ce^{-e[-B(t-M)]}$$

(1)

where *L*(*t*) = log counts of bacteria at time *t* (log (CFU/ml)), *A* = asymptotic log count of bacteria as *t* decreases indefinitely (log (CFU/ml)), *C* = asymptotic log count of bacteria as *t* increases indefinitely (log (CFU/ml)), *M* = time at which the absolute growth rate is maximum (hours), *B* = relative growth rate at *M* ((log (CFU/ml))/h), and *t* = time (hours) and where (4):

$$B = \frac{\log 2 \cdot e}{\text{GT} \cdot C}$$

(2)

$$M = \text{LPD} + \frac{1}{B}$$

(3)

Using the Gompertz primary model and the response surface secondary model from the PMP, log counts were predicted for conditions and times matching every experimental data point from the described data sources, given the initial log counts for the respective experimental growth curve.

Confidence intervals (95%) were generated on the basis of the following equation (adapted from Neter et al. (17)):

$$\text{CI} = \hat{y}_j \pm (z)(\text{SEC})$$

(4)

where CI = confidence interval, *y_j* = predicted value of *j*th data point (log(CFU/ml)), *z* = *z*(1 − α/2), α = 0.05, and SEC = standard error of calibration (formula below).

Robustness index. The RI for the PMP broth-based *L. monocytogenes* growth model was calculated on the basis of the following equation (6):

$$\text{RI} = \text{SEP}/\text{SEC}$$

(5)

where SEC = standard error of calibration.

$$\text{SEC} = \sqrt{\frac{\sum_{i=1}^n (y_i - \hat{y}_i)^2}{n}}$$

(6)

where *y_i* = predicted value of *i*th data point (log(CFU/ml)); *y_i* = observed value of the *i*th data point from the original data sets used to develop the model (log(CFU/ml)), assuming 1 CFU/ml = 1 CFU/g; *n* = number of observed data points from the original data set; and SEP = standard error of prediction.

$$\text{SEP} = \sqrt{\frac{\sum_{j=1}^n (y_j - \hat{y}_j)^2}{n}}$$

(7)

where *y_j* = predicted value of *j*th data point (log(CFU/ml)); *y_j* = observed value of the *j*th data point from an independent data set

TABLE 3. *RI values for conditions inside the PMP model domain*

Data set no.		Product type	Temp (°C)	pH ^a	a _w ^b	Atmosphere	RI	Mean relative error (RE)
1	Ground beef		4	5.8	0.997	Anaerobic	2.44	−0.33
2	Ground beef		4	5.8	0.997	Aerobic	2.21	−0.27
3	Ground beef		4	5.8	0.997	Aerobic	2.18	−0.25
4	Ground beef		10	5.8	0.997	Anaerobic	2.57	−0.39
5	Ground beef		10	5.8	0.997	Aerobic	2.65	−0.25
6	Ground beef		10	5.8	0.997	Aerobic	2.52	−0.28
7	Cooked chicken		3.5	6	0.997	Anaerobic	1.15	−0.16
8	Cooked chicken		3.5	6	0.997	Anaerobic	2.10	−0.32
9	Cooked chicken		6.5	6	0.997	Anaerobic	0.45	0.02
10	Cooked chicken		6.5	6	0.997	Anaerobic	0.78	−0.07
11	Cooked chicken		10	6	0.997	Anaerobic	0.98	−0.08
12	Cooked chicken		10	6	0.997	Anaerobic	1.52	−0.18
13	Pate		6.8	5.6	0.997	Aerobic	0.37	−0.03
14	Cooked pork		4	6.3	0.997	Anaerobic	1.40	−0.21
15	Cooked pork		4	6.2	0.997	Aerobic	1.20	−0.15
16	Cooked pork		20	6.3	0.997	Anaerobic	0.95	−0.12
17	Cooked pork		20	6.2	0.997	Aerobic	1.41	−0.14
18	Cooked pork		20	6.3	0.997	Aerobic	0.66	−0.07
19	Precooked beef		4	6	0.997	Vacuum ^c	1.40	−0.16
20	Precooked beef		4	6	0.997	Vacuum ^c	0.41	−0.04
21	Precooked beef		4	6	0.997	Vacuum ^c	2.76	−0.40
22	Precooked beef		4	6	0.997	Vacuum ^c	1.94	−0.27
23	Precooked beef		4	6	0.997	Vacuum ^c	3.96	−0.58
24	Precooked beef		4	6	0.997	Vacuum ^c	2.36	−0.34
25	Cooked beef w/gravy		5	6	0.997	Aerobic	0.48	0.06
26	Cooked beef w/gravy		10	6	0.997	Aerobic	0.93	−0.08
27	Cooked beef w/gravy		5	6	0.997	Aerobic	1.41	−0.26
28	Cooked beef w/gravy		10	6	0.997	Aerobic	1.95	−0.24
29	Home-style salad (chicken with no mayonnaise added)		4	6	0.997	Aerobic	0.53	0.11
30	Home-style chicken salad		4	6	0.997	Aerobic	0.56	0.08
31	Home-style salad (real mayonnaise + chicken)		4	6	0.997	Aerobic	1.29	−0.23
32	Home-style salad (reduced-calorie mayonnaise + chicken)		4	6	0.997	Aerobic	1.47	−0.27
33	Home-style salad (real mayonnaise + chicken)		12.8	5	0.997	Aerobic	2.08	0.52
34	Home-style salad (reduced-calorie mayonnaise + chicken)		12.8	5	0.997	Aerobic	1.28	0.31
35	Turkey		7	6	0.99	Anaerobic	1.16	−0.19
36	Turkey		7	6	0.99	Aerobic	1.52	−0.19
37	Turkey		7	6	0.99	Aerobic	1.78	−0.21
38	Pork		7	6	0.99	Aerobic	2.45	−0.30
39	Pork		7	6	0.99	Anaerobic	2.87	−0.45
40	Pork		7	6	0.99	Aerobic	3.45	−0.41
41	Pork		7	6	0.99	Aerobic	3.44	−0.40

^a Assumed values for data sets 7–12.
^b Assumed values for data sets 1–34
^c Assumed anaerobic for calculations.

(log(CFU/ml)), assuming 1 CFU/ml = 1 CFU/g; and n = number of observed data points from an independent data set.

The overall RI for each product type was calculated using the combined observed data from all independent sources:

$$RI = \frac{\sqrt{\frac{\sum_{k=1}^n (y_k - \hat{y}_k)^2}{n}}}{SEC}$$

(8)

where \hat{y}_k = predicted value of k th data point (log(CFU/ml)); y_k = observed value of the k th data point from all independent data sets corresponding to each product type (log(CFU/ml)), assuming

1 CFU/ml = 1 CFU/g; and n = total number of observed data points from all independent data sets corresponding to each product type.

Additionally, the mean RE was calculated on the basis of the following formula (6):

$$RE = \frac{\sum_{j=1}^n \left(\frac{y_j - \hat{y}_j}{\hat{y}_j} \right)}{n}$$

(9)

where \hat{y}_j = predicted value of j th data point (log(CFU/ml)); y_j = observed value of the j th data point from an independent data set

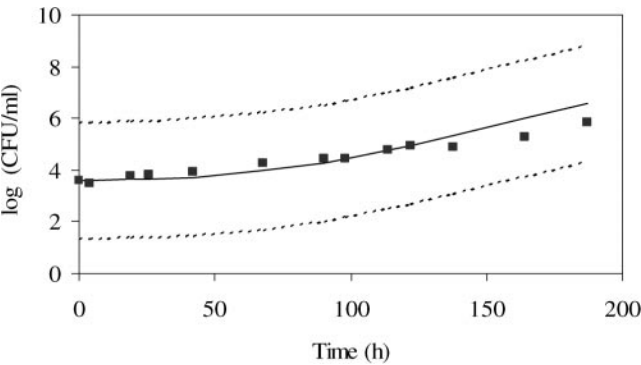


FIGURE 1. Comparison of the predicted (solid line) and actual (full squares) growth log counts from the data set (no. 13) resulting in the best RI value (0.37) inside the PMP model domain (95% confidence intervals, broken lines).

(log(CFU/ml)), assuming 1 CFU/ml = 1 CFU/g; and n = number of data points.

To evaluate whether any of the product/process variables affected the RI, an analysis of variance (ANOVA) was conducted using JMP (version 4.0.4, SAS Institute Inc., Cary, N.C.).

RESULTS AND DISCUSSION

The standard error of calibration values for the PMP growth models for anaerobic and aerobic conditions were 1.49 and 1.15 log (CFU/ml), respectively. This means that the model predictions were within ±1.30 log (CFU/ml) accuracy, on average, for the broth-based data for both atmospheric conditions.

The RI values for all the meat and poultry products that were inside the PMP domain were between 0.37 and 3.96 (Table 3). The mean RE shows that the PMP growth model overpredicted (i.e., fail-safe) the log counts for 85% of the cases.

For the data set yielding the best RI value (Fig. 1), predicted and actual log counts were within the confidence levels, which implies that the model performed better than expected. On the other hand, for the data set yielding the worst RI value (Fig. 2), the actual log counts were outside the confidence bands predicted. This particular data set presented no growth in the total period that was studied.

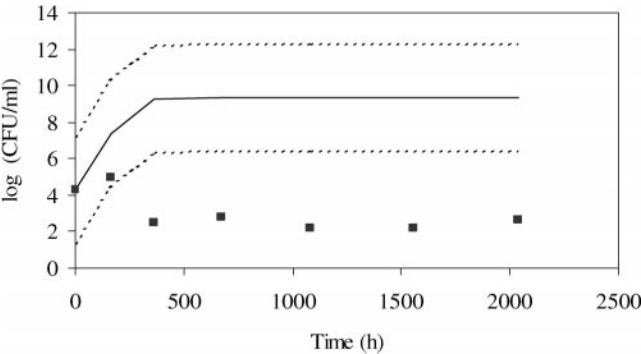


FIGURE 2. Comparison of the predicted (solid line) and actual (full squares) growth log counts from the data set (no. 23) resulting in the worst RI value (3.96) inside the PMP model domain (95% confidence intervals, broken lines).

TABLE 4. ANOVA results for RI versus product and process variables

Variable	P value
Product type	0.0004
pH	0.1484
Temp	0.0975
Atmopshere ^a	0.2856

^a Atmosphere: aerobic or anaerobic

Among the variables tested, only product type affected the RI value (Table 4). Therefore, the data were grouped into classes of similar product type, and an overall performance (RI) was calculated for each group (Table 5). The RI values between 0 and 2 (i.e., pate, cooked chicken, cooked pork, and turkey) indicated satisfactory robustness for the PMP in the application. In other words, the actual log counts were generally within the range described by the standard error of calibration of the model. The RI values above 2 (i.e., pork, ground beef, and precooked beef) suggest that actual log counts are more likely to fall outside the confidence limits of the model for this particular type of meat, and under these specific conditions, the model did not perform as expected.

For data sets under experimental conditions outside the PMP domain (i.e., low temperature), RI values were between 0.40 and 1.22 (Table 6). Again, for these data sets, the PMP growth model overpredicted (i.e., fail-safe) the log counts for most of the cases (83%). The ANOVA of these data showed no significant influence of the experimental conditions on the RI values, probably due to the lack of variation in those variables. As was the case for data within the model domain, for the best RI value, actual and predicted log counts fell within the confidence intervals (Fig. 3). For the data set yielding the worst RI value, the PMP growth model still performed as expected; most of the actual log counts fell within its confidence bands (Fig. 4), because the RI was still approximately 1.20. It should be noted that this evaluation of the model performance in an extrapolated domain was very limited, both in terms of the number and domain of the data. Extrapolation of predictive microbial models is always undesirable and not recom-

TABLE 5. Overall RI values for each product type inside the PMP domain

Product type	Atmosphere	RI
Ground beef	Anaerobic	2.20
	Aerobic	3.10
Cooked chicken	Anaerobic	1.25
	Aerobic	0.30
Cooked pork	Anaerobic	1.10
	Aerobic	1.08
Precooked beef	Vacuum	2.40
Turkey	Anaerobic	1.07
	Aerobic	1.63
Pork	Anaerobic	2.80
	Aerobic	3.40

TABLE 6. *RI* values for conditions outside the PMP model domain

Data set no.	Product type	pH	Temp (°C)	a _w	Nitrite (ppm)	Salt (%)	RI	Mean relative error (RE)
42	Pate or ham	6.2	2	0.991	81.2	1.6	0.78	−0.03
43	Pate or ham	6.2	2	0.991	81.2	1.6	0.93	−0.05
44	Pate or ham	6.2	2	0.991	81.2	1.6	0.70	−0.07
45	Pate or ham	6.2	2	0.991	81.2	1.6	0.70	−0.06
46	Pate or ham	6.2	2	0.991	81.2	1.6	0.91	−0.11
47	Pate or ham	6.2	2	0.991	81.2	1.6	1.22	−0.10
48	Pate or ham	6.2	0	0.991	81.2	1.6	1.15	−0.03
49	Pate or ham	6.2	0	0.991	81.2	1.6	0.40	−0.06
50	Pate or ham	6.2	0	0.991	81.2	1.6	0.69	−0.09
51	Pate or ham	6.2	0	0.991	81.2	1.6	0.85	−0.10
52	Pate or ham	6.2	0	0.991	81.2	1.6	0.69	−0.10
53	Pate or ham	6.2	0	0.991	81.2	1.6	0.81	−0.14
54	Pate or ham	6.3	2	0.989	103	2.0	1.10	−0.03
55	Pate or ham	6.3	2	0.989	103	2.0	0.70	0.01
56	Pate or ham	6.3	2	0.989	103	2.0	0.78	−0.05
57	Pate or ham	6.3	2	0.989	103	2.0	0.57	−0.04
58	Pate or ham	6.3	2	0.989	103	2.0	0.87	−0.07
59	Pate or ham	6.3	2	0.989	103	2.0	0.93	−0.02
60	Pate or ham	6.3	0	0.989	103	2.0	0.47	−0.02
61	Pate or ham	6.3	0	0.989	103	2.0	0.62	0.00
62	Pate or ham	6.3	0	0.989	103	2.0	0.85	0.07
63	Pate or ham	6.3	0	0.989	103	2.0	0.70	0.07
64	Pate or ham	6.3	0	0.989	103	2.0	0.86	−0.11
65	Pate or ham	6.3	0	0.989	103	2.0	0.97	−0.07

mended; however, the RI is one possible method for evaluating the performance of models both within and outside the original calibration domain.

To avoid dangerous errors when using growth models for risk assessment (or other application), predictive models should be validated against independent data relevant to the application. In prior studies, the broth-based PMP growth model for *Escherichia coli* O157:H7 underpredicted (i.e., fail-dangerous) microbial counts when compared to data in ground beef (6, 22, 23). Similar results were reported in the PMP for the *Clostridium perfringens* growth model against data from broth (21). In the present study, the broth-based PMP growth model for *L. monocytogenes* performed

reasonably well overall for meat and poultry products, both inside and outside its original domain. In other words, it is a robust model for growth predictions that can be applied to meat and poultry products. Moreover, in some cases, the model performed better than expected (RI was approximately 0 to 1). In general, microbial counts for *L. monocytogenes* were overpredicted by the PMP growth model. However, the data outside the model domain were limited to a very small range (i.e., low temperature and just one product); future work should further evaluate models in a broader domain of extrapolation and generate more experimental data to widen the validated domain of predictive models.

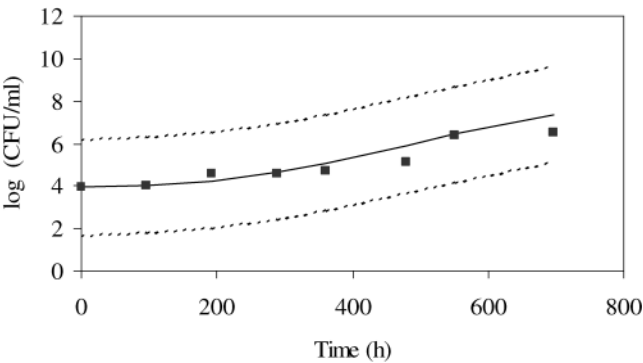


FIGURE 3. Comparison of the predicted (solid line) and actual (full squares) growth log counts from the data set (no. 48) resulting in the best RI value (0.40) outside the PMP model domain (95% confidence intervals, broken lines).

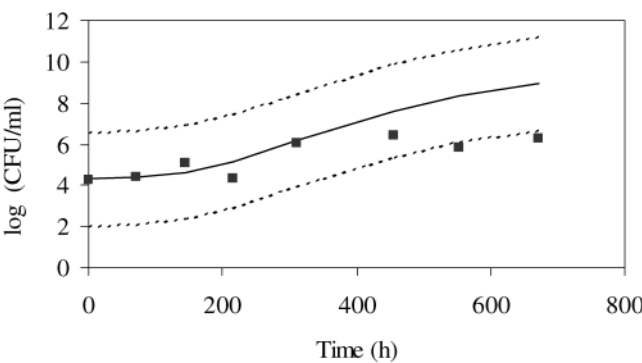


FIGURE 4. Comparison of the predicted (solid line) and actual (full squares) growth log counts from the data set (no. 46) resulting in the worst RI value (1.22) outside the PMP model domain (95% confidence intervals, broken lines).

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